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Stimulation of Black Spruce Germination by Osmotic Priming: Laboratory Studies

R. L. Fleming and S. A. Lister

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STIMULATION OF BLACK SPRUCE GERMINATION BY OSMOTIC PRIMING: LABORATORY STUDIES

R.L. FLEMING AND S.A. LISTER[1]

GREAT LAKES FOREST RESEARCH CENTRE

CANADIAN FORESTRY SERVICE

DEPARTMENT OF THE ENVIRONMENT

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ABSTRACT

Osmotic priming increased the vigor, speed, and in some cases uniformity of black spruce (*Picea mariana* [Mill.] B.S.P.) germination, particularly at low temperatures. The best priming treatments decreased the time to 50% germination (T50) by 14 days at 10°C germination temperature, by 3 days at 21°C, and by 5 days at 32°C. Seed treatment had no adverse effect on germination capacity or seedling development. Osmotically primed seed can be stored at low temperatures (0.5°C) and moisture contents (6%) for up to 56 days and still retain most of the benefits of priming. However, storage for longer periods or at higher temperatures and moisture contents may reduce seed quality. Forty-eight priming combinations of soaking time, temperature and solute concentration, and 4 seedlots, were tested.

RÉSUMÉ

Le prétraitement des graines d'épinette noire (*Picea mariana* [Mill.] B.S.P.) en présence d'agents osmotiques a accru la vigueur, la rapidité et, dans certains cas, l'uniformité de leur germination, spécialement aux basses températures. Avec les meilleurs traitements, le temps nécessaire pour obtenir la germination de 50% des graines (T50) a été réduit de 14 jours à 10°C, de 3 jours à 21°C et de 5 jours à 32°C. On n'a pas observé d'altération de la faculté germinative et du développement des semis. Après leur prétraitement, les graines peuvent être conservées à de basses températures (0.5°C) et sous une faible humidité (6%) jusqu'à 56 jours et conserver la majeure partie des avantages du prétraitement. Toutefois, une conservation plus longue ou sous une température et une humidité plus élevées peut entraîner une perte de qualité des semences. Les essais ont porté sur 48 combinaisons de conditions de prétraitement (durée de trempage, température et concentration de soluté) et 4 lots de graines.

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INTRODUCTION

Germination of black spruce *(Picea mariana* [Mill.] B.S.P.) seed on boreal forest cutovers and in northern Ontario nurseries can be slow, uneven and erratic. In nursery beds resulting differences in the duration of first-year growth contribute to stock variability, and consequently to problems with culling and stock handling (Skeates 1980). On cutover sites delays in germination increase the risk of seed destruction or loss of viability through moisture stress, temperature extremes, seed burial and seed predation. As well, seeds germinating later in the growing season may produce smaller first-year seedlings less capable of withstanding high temperatures, drought, frost heaving and competition from surrounding vegetation (Larson 1963).

Osmotic priming[2] (Heydecker 1974) has considerable potential as a treatment to improve the germinative speed and/or capacity of tree seed. Studies have shown that it can promote rapid, synchronous germination of agricultural species, is relatively inexpensive and simple to apply, and is adaptable to different situations (Heydecker et al. 1973, 1975, Salter and Darby 1976, Bodsworth and Bewley 1981, Khan et al. 1981).

Osmotic priming involves imbibing seeds in an aqueous polyethylene glycol (PEG) solution of a given negative solute water potential. Through control of solute concentration, temperature and duration of soaking, the seed is permitted to undertake initial germination processes such as the mobilization of food reserves, RNA synthesis and accumulation (Coolbear et al. 1980), and the formation of enzyme systems, but not to begin radicle emergence. If we assume that these initial processes are irreversible, more rapid germination should occur when seeds are 'primed' before sowing. More uniform germination may also result if variations in germination rate largely reflect differences in the time needed to complete these early stages (Heydecker 1974).

This report outlines the effects of osmotic priming on germination and early seedling growth of black spruce under controlled conditions.

METHODS AND RESULTS

A series of five experiments was carried out to examine the effects of osmotic priming. Procedures common to all or several experiments are reported in the next section. Results and any additional information on procedures are reported separately for each experiment.

General Methods and Materials

Seed was obtained from the Ontario Tree Seed Plant as bulk seedlots, identified by site region (Hills 1960) and collection number. Seeds were surface sterilized by immersion in a 16.7% Javex solution (1% solution of active Cl^-) for 10 seconds, rinsed, and air-dried overnight before treatment or, in the case of controls, before sowing.

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[2] The terms 'osmotic priming' and 'priming' are used interchangeably in this report.

Four 100-seed replicates were used per treatment in all controlled-temperature germination trials. Seeds were placed on saturated, short-grain black germination paper overlying bleached Kimpak[3] in covered, sterilized petri dishes and were incubated under low-level incandescent light at constant (± 0.5°C) cardinal germination temperatures for black spruce (Fraser 1970). A seed was considered germinated when the radicle reached 2 mm in length, or in the case of sowing on peat-vermiculite mixtures, when the seed coat was freely suspended above the surface. Germination was tallied daily for 28 days at 21°C and 32°C, and for 45 days at 10°C, after which cut tests were performed on all seeds that had not germinated to determine whether they were full, empty or damaged.

In growth chamber and greenhouse experiments six 50-seed replicates were used per treatment. Seeds were surface sown on a 2:1 peat-vermiculite mixture, lightly top dressed with silica grit, and moistened daily. Greenhouse temperatures at bench level ranged from 21-23°C (day) to 18-20°C (night). The greenhouse bench and the growth chamber were lighted 16 hours a day. Seedlings were fertilized every second day with 50 ppm of 20-20-20 NPK fertilizer after they had developed primary needles.

Priming involved placing seeds in covered circular petri dishes containing three No. 1 Whatman filter papers presoaked with 6 ml of solutions containing various concentrations of polyethylene glycol (PEG 6000). Solute water potentials were calculated according to Michel and Kaufmann (1973). The dishes were placed in covered glass jars containing a small amount of water to reduce evaporation, and incubated at 10, 15 or 20°C with low-level, continuous incandescent lighting for 3, 7, 14 or 28 days. The seeds were then rinsed with distilled water and air dried 24 hours at room temperature before sowing.

The effects of treatment on germination were examined in terms of germinative capacity (the percentage of sound seed that germinated), uniformity of effective germination (time from the beginning of germination until 90% of the viable seed had germinated), germinative speed (T50-days from sowing to 50% germination of the viable seed: the lower the value of T50 the greater the germinative speed), and germinative vigor (peak value--the highest value for cumulative germination/days since sowing [Czabator 1962]).

All data were analyzed by one-way analysis of variance techniques, and individual differences between treatments were established using Tukey's multiple comparison test. Results are reported as mean values per treatment.

Experiment 1. Effect of Various Priming Treatments on the Germination of One Seedlot

The effectiveness of any particular priming treatment (solute concentration - imbibition time - soaking temperature combination) in improving germination characteristics depends on the species involved. Seeds of some species respond best to fairly dilute concentrations and/or lengthy imbibition periods, while those of other species require shorter periods and higher concentrations; the

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[3] Mention of commercial products and company trade names does not constitute endorsement of either by the Great Lakes Forest Research Centre.

optimum treatment combination must be established separately for each species. In this first experiment we examined a wide variety of treatment combinations to determine those with the greatest potential for black spruce (Table A1). The combinations examined included a number that have proven successful with other plant species (cf. Heydecker 1974, Heydecker et al. 1973, 1974, 1975, Simak 1976, Akalehiywot and Bewley 1977).

None of the priming treatments tested had a meaningful effect on germinative capacity, which was at least 95% for all treatments (including controls) at all three germination temperatures for this high-quality seedlot from Site Region 3W (seedlot A). However, a number of treatments resulted in faster, more vigorous germination at each germination temperature (Tables A1-A6). The best treatments also resulted in significantly more uniform germination at 10°C and 32°C, but not at 21°C (Tables A7-A9).

Increases in imbibition time and temperature during treatment generally had a positive effect on germinative speed, vigor and uniformity. The greatest benefits were obtained by imbibing seed in solutions of high negative water potential for long periods at higher temperatures (i.e., -1250 kPa, 21 days, 15°C and -1250 kPa, 14 days, 20°C). These were treatments which allowed the seed to progress farthest towards germination without allowing radicle emergence. However, when conditions were too favorable the seed germinated during priming (i.e., -1000 kPa, 14 days, 20°C, and -1250 kPa, 21 days, 20°C).

The best treatments decreased T50 by 3 days at 21°C, 5 days at 32°C, and 14 days at 10°C, and improved germination uniformity by 4 days at 10°C and 32°C.

Experiment 2. Effect of Priming Treatments on Additional Seedlots

This second experiment was conducted to determine whether bulk seedlots of black spruce collected at different times and from different Ontario locations were likely to respond similarly to priming. Could a single priming treatment be used effectively with different seed collections or would priming treatments have to be tailor-made for each seedlot?

Six treatments (Table 1) from Experiment 1 which improved speed and vigor and represent a range of solute concentration, imbibition temperature, and

Table 1. Osmotic priming treatments used in Experiment 2.

Treatment number	Solute concentration (kPa)	Imbibition temperature (°C)	Imbibition time (days)
1	-750	10	21
2	-1000	10	21
3	-1000	15	14
4	-1250	15	14
5	-1250	15	21
6	-1250	20	14

imbibition time were applied to three additional seedlots, two from Ontario site region 3E (seedlots B, C) and one from Ontario site region 3W (seedlot D).

None of the treatments had a meaningful effect on germinative capacity; over 96% of the sound seed germinated in all cases. However, priming seedlots C and D at -1250 kPa, 20°C, for 14 days resulted in considerable ($\geq$ 10%) premature radicle emergence.

All other treatments promoted faster, more vigorous germination at both germination temperatures (tables 2 and 3). T50 decreased by as much as 14 days at 10°C and 4 days at 21°C. There was little practical difference in the uniformity of germination at 21°C, but at 10°C some priming combinations improved uniformity for all seedlots (Table 4). Generally the treatments which improved germinative speed and vigor the most with these seedlots also produced the largest gains with seedlot A.

Experiment 3. *Effect of Priming on Germination and Seedling Growth Under Greenhouse and Growth Chamber Conditions.*

To determine whether similar improvements in germination characteristics could be obtained on a different seedbed medium and to examine early seedling growth, a greenhouse and growth chamber study was established using seedlot A. Three priming treatments were tested (treatments 3, 5 and 6 from Experiment 2) in petri dishes and on a peat-vermiculite mixture in a growth chamber at 20°C, and on peat-vermiculite in the greenhouse.

Table 2. Experiment 2: Effect of priming treatment on T50 (days) of seedlots B, C, and D at 10°C and 21°C germination temperatures.

Seedlot	Germin. temp.	Treatment number 1	2	3	4	5	6	Untreated seed
B	10°C	9.8cd	13.3e	10.8d	8.8bc	7.3a	8.3ab	23.3f
	21°C	3.8b	4.0b	3.0a	3.0a	3.0a	2.5a	6.8c
C	10°C	9.5b	11.0c	9.0b	9.0b	7.3a	X[a]	22.0d
	21°C	3.0a	3.8b	3.0a	3.0a	3.0a	X	6.0c
D	10°C	9.0b	10.0c	10.0c	9.0b	7.0a	X	21.0d
	21°C	3.0b	3.3b	3.0b	3.0b	2.3a	X	6.0c

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter in the same row.

Table 3. Experiment 2: Effect of priming treatment on peak values of seedlots B, C, and D at 10°C and 21°C germination temperatures.

Seedlot	Germin. temp.	Treatment number 1	2	3	4	5	6	Untreated seed
B	10°C	6.7cd	6.1c	4.5b	7.4d	10.0f	8.8c	3.1a
	21°C	20.8bc	18.8b	23.1c	24.2c	30.9d	30.4d	12.0a
C	10°C	8.1d	6.5b	7.2c	7.9d	11.6c	X[a]	3.7a
	21°C	24.4b	22.8b	28.6c	26.9c	32.8d	X	13.8a
D	10°C	8.1c	7.0b	6.8b	8.1c	11.9d	X	3.9a
	21°C	26.4c	23.7b	29.9d	29.1d	32.3e	X	14.0a

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter in the same row.

Table 4. Experiment 2: Effect of priming treatment on uniformity of effective germination (days) of seedlots B, C, and D at 10°C and 21°C germination temperatures.

Seedlot	Germin. temp.	Treatment number 1	2	3	4	5	6	Untreated seed
B	10°C	8.8bc	15.8c	11.5cd	9.5bc	4.5a	7.0ab	14.5d
	21°C	4.0b	3.8b	3.3b	3.5b	2.0a	2.0a	4.0b
C	10°C	6.8bc	8.3c	8.5c	6.5b	3.0a	X[a]	8.5c
	21°C	3.0a	3.0a	3.0a	3.0a	2.0a	X	3.0a
D	10°C	6.5ab	7.8b	10.5c	6.8ab	4.0a	X	7.5b
	21°C	3.0b	2.8ab	2.5ab	2.5ab	2.0a	X	3.0b

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter in the same row.

Findings from these studies were similar to those from the two previous trials; priming improved germinative speed and vigor (Tables A10 and A11) but had little effect on germination capacity or uniformity at 20°C.

The initial advantage of primed seed, in terms of faster germination, was maintained to the primary needle stage: seedlings developing from primed seed lost their seedcoats and entered the primary needle stage 3-5 days earlier. However, after 10 weeks in the greenhouse the heights and dry weights (shoot and root) of seedlings from primed seed were not significantly larger. Coefficients of variation in height increment among seedlings of the same replicate varied from 0.17 to 0.39, and were as high as 0.21 between mean values per replicate for the same treatment. This large variability in seedling growth within and between replicates made it more difficult to distinguish treatment effects.

Experiment 4. Further Effects of Priming on Germination and Seedling Growth Under Greenhouse and Growth Chamber Conditions

To investigate further the effects of priming on germination and early seedling growth under different conditions, a 10-week greenhouse and 14-week growth chamber experiment using one priming treatment (-750 kPa, 10°C, 21 days) was conducted with seedlot A. Spring field temperatures were simulated in the growth chamber. Weekly mean, weekly mean maximum, and weekly mean minimum temperatures were calculated from temperature data collected 1.3 m above the ground from 15 May to 21 August, 1979 on an upland black spruce cutover 90 km north of Thunder Bay, Ontario. The weekly mean maximum and weekly mean temperatures were averaged, as were the weekly mean and weekly mean minimum, and the growth chamber was set at each of these two temperatures for 12 hours per day. Temperature settings were adjusted weekly to correspond with these data (Table 5).

Table 5. Growth chamber temperatures used in Experiment 4.

	Week number													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
High temp. (°C)	10	14	15	15	21	15	18	22	22	22	20	17	16	16
Low temp. (°C)	5	7	7	9	13	8	12	14	16	15	14	13	10	11

Priming again resulted in faster, more vigorous germination but did not influence germination capacity or uniformity (Tables 6 and 7). In the growth chamber, where temperatures approximated field conditions more closely, T50 was decreased by 10 days. This compares with a decrease of 12 days for the same treatment at 10°C (Experiment 1). The seedlings which developed from primed

Table 6. Experiment 4: Effect of priming on T50 (days) of seedlot A in growth chamber (varied temperatures) and greenhouse environments.

Location	Primed seed	Untreated seed
Growth chamber	14.5c	24.2d
Greenhouse	5.8a	8.3b

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table 7. Experiment 4: Effect of priming on peak values of seedlot A in growth chamber (varied temperatures) and greenhouse environments.

Location	Primed seed	Untreated seed
Growth chamber	2.6b	1.7a
Greenhouse	7.2d	5.0c

There is no significant difference (P = 0.05) between values with the same lower case letter.

seed shed their seedcoats sooner and developed primary needles earlier (by 9 and 3 days in the growth chamber and greenhouse, respectively). However, at the end of 14 weeks in the growth chamber they did not exhibit significant increases in height or dry weight over seedlings that developed from untreated seed. As before, there were large variations in size among seedlings of the same replicate and between replicates of the same treatment.

Experiment 5. Storage of Primed Seed

While priming holds considerable promise for improving germination rates when seed is sown immediately after treatment, in many instances treated seed must be stored before sowing. Storage of primed agricultural and horticultural seed may partially negate many of the advantages of priming (Heydecker and Wainwright 1976, Bodsworth and Bewley 1981). To determine the effects of storage on primed black spruce seed, an experiment was conducted using two seedlots (seedlots B and E), two priming treatments (-1000 kPa, 10°C, 21 days; and -1250 kPa, 15°C, 14 days), two storage treatments, and storage periods of 0, 7, 14, 28 and 56 days. Following priming, seeds were rinsed, air-dried at room temperature for 24 hours and then placed in a vacuum desiccator to reduce moisture content to approximately 6%. Half the treated seed was then stored at 0.5°C in sealed containers (Wang 1974), while the other half, together with an untreated control, was left uncovered on a laboratory shelf at room temperature.

Storage for up to 56 days had no significant effect on germination capacity at 21°C. However, primed seed from three of the four treatment-seedlot combinations left at room temperature for 56 days, and from one of the combinations left at room temperature for 28 days, suffered significant reductions in germination capacity at 10°C (Table 8). By contrast, the germination capacity of both untreated and cool-stored, treated seed was not significantly affected by storage.

There was a gradual decline in germinative speed at 10°C with increased duration of storage at 0.5°C, and a marked decline with storage at room temperature (Table 9). At 21°C germination temperature, similar trends occurred but were less marked. Storage of untreated seed at room temperature for up to 28 days had no effect on germinative speed, but 56-day storage sometimes resulted in a significant decline.

Table 8. Experiment 5: Effect of storage of primed seed from seedlots B and E on germination capacity at 10°C germination temperature.

Seedlot	Storage time (days)	Storage temperature (°C)	Treatment 1	Treatment 2	Untreated seed
B	Treated seed, no storage		96.5bc	94.8cd	
	Untreated seed, no storage		93.8b	93.8cd	93.8a
	7	0.5	97.3bc	95.0cd	
		room	97.5bc	94.3cd	89.8a
	14	0.5	99.5c	93.8cd	
		room	97.8bc	90.0c	93.8a
	28	0.5	98.3bc	96.8cd	
		room	95.3bc	64.8b	93.5a
	56	0.5	96.8bc	98.0d	
		room	88.5a	36.8a	95.0a
E	Treated seed, no storage		96.0a	98.5b	
	Untreated seed, no storage		94.0a	94.0b	94.0a
	7	0.5	97.0a	94.5b	
		room	96.5a	95.5b	95.8a
	14	0.5	98.5a	97.5b	
		room	99.3a	96.8b	90.0a
	28	0.5	95.3a	97.5b	
		room	96.0a	93.5b	93.8a
	56	0.5	97.3a	96.0b	
		room	95.0a	82.8a	91.0a

There is no significant difference (P = 0.05) between values with the same lower case letter in any given column for each seedlot.

The germinative vigor (peak values) (Table 10) and uniformity of germination of primed seed stored at 0.5°C slowly decreased over time, while that of primed seed stored at room temperature declined markedly. In general, similar trends were apparent at germination temperatures of 10°C and 21°C, but differences were most marked at 10°C. Storage of untreated seeds at room temperature for up to 56 days had no significant effect on germinative vigor or uniformity of germination.

Table 9. Experiment 5: Effect of storage of primed seed from seedlots B and E on T50 (days) at 10°C germination temperature.

Seedlot	Storage time (days)	Storage temperature (°C)	Treatment 1	Treatment 2	Untreated seed
B	Treated seed, no storage		12.3a	8.8a	
	Untreated seed, no storage		24.0d	24.0e	24.0a
	7	0.5	12.0a	9.5ab	
		room	12.5a	9.8a-c	26.5a
	14	0.5	12.5a	11.0bc	
		room	14.3b	14.5d	25.8a
	28	0.5	13.3ab	9.3a	
		room	19.5c	23.5e	28.5a
	56	0.5	14.3b	11.3c	
		room	23.3d	30.8f	21.7a
E	Treated seed, no storage		14.0a	11.0ab	
	Untreated control, no storage		26.8f	26.8e	26.8a
	7	0.5	14.8ab	9.3a	
		room	15.3ab	10.3a	28.5ab
	14	0.5	15.0ab	10.8ab	
		room	16.5bc	13.3b	30.8c
	28	0.5	16.5bc	11.3ab	
		room	20.3d	16.3c	29.5bc
	56	0.5	18.5cd	11.5ab	
		room	23.3e	22.3d	29.0bc

There is no significant difference (P = 0.05) between values with the same lower case letter in any given column for each seedlot.

Table 10. Experiment 5: Effect of storage of primed seed from seedlots B and E on peak values at 10°C germination temperature.

Seedlot	Storage time (days)	Storage temperature (°C)	Treatment 1	Treatment 2	Untreated seed
B	Treated seed, no storage		4.8e	6.8f	
	Untreated seed, no storage		2.5ab	2.5b	2.5b
	7	0.5	4.5e	6.6fg	
		room	4.2de	5.5de	2.3ab
	14	0.5	4.8e	5.3de	
		room	3.5c	3.9c	2.4ab
	28	0.5	4.2de	6.2ef	
		room	3.0bc	1.6ab	2.1a
	56	0.5	3.6cd	5.1d	
		room	2.2a	0.8a	2.4b
E	Treated seed, no storage		4.1f	5.4ef	
	Untreated seed, no storage		2.3a	2.3ab	2.3a
	7	0.5	4.1f	5.7f	
		room	3.8ef	5.2d-f	2.3a
	14	0.5	4.1f	5.3d-f	
		room	3.5de	4.1c	2.0a
	28	0.5	3.4de	4.7c-e	
		room	2.9bc	3.1b	2.2a
	56	0.5	3.1cd	4.5cd	
		room	2.6ab	2.2a	2.1a

There is no significant difference (P = 0.05) between values with the same lower lower case letter in any given column for each seedlot.

Over all, treated seed stored at 0.5°C and 6% moisture content for up to 56 days showed no decline in viability or uniformity of germination, and retained better germinative speed and vigor than untreated seed. However, primed seed stored at room temperature and ambient moisture showed a marked decline in viability after 28 to 56 days' storage, particularly at 10°C germination temperature. As well, the speed, vigor and uniformity of germination of this seed were little better, and on some occasions poorer, than that of untreated seed.

DISCUSSION AND CONCLUSIONS

Results of these trials indicate that osmotic priming can improve the speed, vigor, and sometimes the uniformity of black spruce germination. At least two priming treatments (-1250 kPa, 20°C, 14 days; and -1250 kPa, 15°C, 21 days) can increase T50 by 14 days at 10°C, by 3 days at 21°C, and by 5 days at 32°C. Under greenhouse conditions improvements in germinative speed led to commensurate reductions in the time required (from sowing) for seedlings to develop primary needles.

Osmotic priming had no significant effect on germinative capacity. Virtually all sound seed from each seedlot germinated and grew normally, regardless of treatment. Jackson (1962) and Leshem (1966) found that low molecular weight PEG formulations are toxic to seedling root development in aqueous solutions. There is, however, no evidence that priming with high molecular weight PEG solutions, as in the present studies, reduces seed vitality or seedling development.

With osmotic priming maximum improvements in germination are obtained by allowing the seed to progress as far through the initial stages of germination as possible without permitting radicle emergence (Heydecker et al. 1974). However, small errors in priming procedures with the best treatments (solute concentrations too low, imbibition temperatures too high and/or imbibition times too long) may result in radicle emergence during treatment. Optimum priming treatments also vary somewhat for different seedlots. A treatment that produces the greatest gains with one seedlot may result in premature germination with another. For large-scale application one might compromise by selecting treatments that produce substantial improvements in germinative speed and vigor, and can safely be employed with a wide variety of seedlots. Such treatments are unlikely to improve the uniformity of germination.

Osmotic priming is merely a refined method of soaking seed whereby the progression of germination is more closely controlled. Cold soaking of black spruce seed in water alone will increase the rate of germination (Rudolf 1950). The effect is probably comparable to that obtained with the weakest solute concentration in Experiment 1. The results of Experiment 1 suggest that, through osmotic priming, faster, more vigorous and more uniform germination can be achieved. The advantage of priming over soaking in water is that seeds can be soaked longer at given temperatures, without permitting radicle emergence.

Osmotic priming appears to offer the greatest potential benefits in conditions under which prompt germination at low temperatures is an asset. This is likely the case on boreal upland sites where cool spring temperatures are followed by periods of drought, and on lowland sites where cold temperatures limit seed germination and seedling growth (Kenety 1917). Other factors being equal, seedlings which germinate earlier should be capable of producing larger, more extensive root systems the first year, and thus have a greater capacity to withstand drought, frost heaving and competition from other vegetation. Larson (1963) found significant differences in first-year growth among ponderosa pine (*Pinus ponderosa* Laws.) that germinated as little as a week apart. Those that germinated earlier had larger, deeper, heavier root systems. The importance of prompt, early germination to first-year growth has also been pointed out by Sweet and Wareing (1966), although early germination may increase the risk of late spring frost damage to new germinates.

Factors such as seed size, seed weight, genetic growth potential, seedbed type and microsite, as well as germination characteristics, are major determinants of seedling growth. The significance of each varies with location and reflects the overall conditions of growth. In the greenhouse where moisture, temperature and nutrient regimes are ameliorated, a decrease in T50 by as much as 10 days had no significant effect on seedling size 14 weeks after sowing. The large variation in seedling growth potential (as a result of seed size, weight, genetics, etc.) of black spruce seed from bulk collections likely obscured the effects of improved germination rates. However, in nurseries and on cutovers where conditions for germination, growth and survival are considerably poorer, such improvements in germinative speed may be important. This is an area for further research.

During the present experiments primed seeds were air dried 24 hours before sowing or storage. Research with agricultural species has shown that drying reduces some of the beneficial effects of priming. Maximum gains in germination are obtained by sowing immediately after treatment (Heydecker and Wainwright 1976, Bodsworth and Bewley 1981). Consequently, greater increases in germinative speed and vigor than those reported herein can likely be obtained if primed black spruce seed is sown immediately after rinsing. However, handling will be more difficult because the seedcoats of imbibed seed are relatively soft, and offer the embryo less protection. Primed, air-dried seed can likely be handled, treated and sown in the same fashion and with the same equipment as untreated seed.

Storage is another consideration. It is apparent that the vigor, speed and uniformity of germination of primed seeds declines with storage--gradually when they are stored at 0.5°C and 6% moisture content, and fairly rapidly when they are left at room temperature and humidity. Seeds should be sown as soon as possible after treatment. When storage is necessary it should be at low temperatures and moisture contents.

It may be possible to store treated seed safely for longer periods by incorporating protectants against pathogens into the seed during priming. Likewise, additives such as growth regulators could be incorporated in the osmoticum to promote even better germination and/or seedling growth and development (Khan et al. 1981).

For large-scale applications, seeds can be primed in aerated aqueous solutions (aerobic conditions are necessary) of the required solute concentration (Darby and Salter 1976). Precautions should be taken to ensure that solute water potentials do not increase during treatment through evaporation, and soaking times may need adjustment because seed can imbibe water faster when completely immersed.

Light is also required during treatment. Priming black spruce seeds in darkness had virtually no effect on germination characteristics. Similar results have been reported for certain crop and weed species (Khan and Karssen 1980, Khan et al. 1981). Apparently secondary dormancy can be induced in seeds of some species (those under phytochrome control) which normally germinate in the dark, by prolonged dark treatment under conditions that prevent or limit germination (Khan et al. 1981).

Osmotic priming should not be employed indiscriminately with seed of other tree species. It has been used successfully with Scots pine (*Pinus sylvestris* L.) (Simak 1976), but has failed to enhance substantially the germination of Norway spruce (*Picea abies* [L.] Karst.), sitka spruce (*Picea sitchensis* [Bong.] Carr.) or lodgepole pine (*Pinus contorta* Dougl.) (Anon. 1978). Trials with white spruce (*Picea glauca* [Moench] Voss) are currently being carried out by B.S.P. Wang at the Petawawa National Forestry Institute.

In conclusion:

1) Osmotic priming increased the speed, vigor, and in some cases the uniformity of black spruce germination. The largest gains were obtained with germination at low temperatures.

2) Under the conditions tested, priming had no deleterious effects on germination capacity or first-year seedling growth.

(3) Primed seed was dried back and stored at 0.5°C for up to 56 days without a reduction in germinative capacity and with relatively little deterioration in germinative speed and vigor. However, the germination characteristics of treated seed stored at room temperature and ambient moisture deteriorated with storage. The germinative speed, vigor and capacity of seed stored in this fashion for 56 days were no better, and in some cases were poorer, than those of untreated seed.

4) Variations in the inherent growth potential (as a result of seed weight, genetics, etc.) of seeds from bulk, mass-collected seedlots overshadowed the effects of priming on first-year seedling growth in the greenhouse and growth chamber.

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APPENDIX

Table A1. Experiment 1: Effect of priming treatment on T50 (days) of seedlot A at 10°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (kPA)			
		-500	-750	-1000	-1250
3	10	21.5j	21.5j	21.8j	22.3j
	15	21.3j	21.0ij	21.8j	21.8j
	20	22.8j	21.5j	21.0ij	21.5j
7	10	17.8gh	17.5gh	18.3g-i	19.0hi
	15	14.0de	14.3d-f	15.0ef	16.3fg
	20	X[a]	X	10.5bc	12.3cd
14	10	12.5cd	13.3de	14.5d-f	14.8ef
	15	X	X	8.7ab	9.5ab
	20	X	X	X	7.3a
21	10	X	9.8b	10.5bc	12.8de
	15	X	X	X	7.5a
	20	X	X	X	X

Untreated seed--22.0j

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A2. Experiment 1: Effect of priming treatment on T50 (days) of seedlot A at 21°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	6.0gh	6.0gh	6.0gh	6.0gh
	15	5.8f-h	5.8f-h	6.0gh	6.0gh
	20	5.0d-f	5.0d-f	5.3e-g	5.3e-g
7	10	5.0d-f	5.0d-f	5.5e-h	5.3e-g
	15	4.0bc	4.0bc	4.0b-c	4.3cd
	20	X[a]	X	3.3ab	3.0a
14	10	4.3cd	4.8c-e	5.0d-f	5.0d-f
	15	X	X	3.0a	3.0a
	20	X	X	X	3.0a
21	10	X	4.0bc	4.0bc	4.3cd
	15	X	X	X	3.0a
	20	X	X	X	X

Untreated seed--6.0gh

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A3. Experiment 1: Effect of priming treatment on T50 (days) of seedlot A at 32°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	5.3gh	5.3gh	5.5h	5.3gh
	15	5.3gh	5.3gh	5.3gh	5.3gh
	20	5.3gh	4.8e-h	5.0f-h	5.3gh
7	10	5.0f-h	4.8e-h	5.0f-h	5.3gh
	15	4.0c-f	4.0c-f	4.0c-f	4.3d-g
	20	X[a]	X	3.0a-c	3.0a-c
14	10	3.8c-e	3.8c-e	4.0c-f	4.0c-f
	15	X	X	3.0a-c	3.0a-c
	20	X	X	X	2.0a
21	10	X	3.0a-c	3.0a-c	3.3bc
	15	X	X	X	2.3ab
	20	X	X	X	X

Untreated seed--7.5i

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A4. Experiment 1: Effect of priming treatment on peak values of seedlot A at 10°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	3.7a-d	3.8a-e	3.7a-d	3.6a-c
	15	3.6a-c	3.7a-d	3.7a-c	3.6a-c
	20	2.9a	3.3ab	3.6a-c	3.6a-c
7	10	4.3a-f	4.4a-f	4.1a-e	3.9a-e
	15	4.1a-e	4.8b-f	4.7b-f	4.5a-f
	20	X[a]	X	6.0f-i	5.3c-g
14	10	6.0f-i	5.5e-h	5.2c-g	4.8b-f
	15	X	X	6.7g-i	7.6i
	20	X	X	X	10.1j
21	10	X	7.2hi	6.9g-i	5.4d-h
	15	X	X	X	10.3j
	20	X	X	X	X

Untreated seed--3.60a-c

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A5. Experiment 1: Effect of priming treatment on peak values of seedlot A at 21°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	13.5a	13.9a	13.4a	13.6a
	15	14.4ab	14.8a-c	14.0a	14.2ab
	20	14.4ab	15.3a-d	14.9a-c	14.6a-c
7	10	15.9a-e	15.3a-d	14.8a-c	15.0a-d
	15	20.3f-h	21.2g-i	18.8e-g	17.9d-f
	20	X[a]	X	22.7hi	22.3hi
14	10	17.7c-f	17.2b-e	17.2b-e	15.8a-e
	15	X	X	27.8j	23.6i
	20	X	X	X	31.1k
21	10	X	23.0hi	21.1g-i	20.3f-h
	15	X	X	X	30.0jk
	20	X	X	X	X

Untreated seed--13.75a

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A6. Experiment 1: Effect of priming treatment on peak values of seedlot A at 32°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	13.9cd	14.2c-e	13.3a-c	14.0c-e
	15	13.7cd	14.0cd	14.3c-e	13.8cd
	20	13.5b-d	14.6c-f	15.0c-f	14.3cd
7	10	15.4c-g	15.4c-g	15.0c-f	14.8c-f
	15	18.6f-h	18.6f-h	18.4e-h	16.3c-g
	20	X[a]	X	27.2jk	22.3hi
14	10	21.7hi	21.0hi	19.4g-i	18.0d-h
	15	X	X	31.3k	28.4k
	20	X	X	X	38.31
21	10	X	29.8k	27.8jk	23.7ij
	15	X	X	X	32.3k
	20	X	X	X	X

Untreated seed--9.20ab

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A7. Experiment 1: Effect of priming treatment on uniformity of effective germination (days) of seedlot A at 10°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	9.3b-h	8.3b-e	8.8b-g	8.0b-d
	15	10.5c-h	9.5b-h	9.8b-h	9.8b-h
	20	16.8j	14.3ij	12.0g-i	10.5c-h
7	10	10.0c-h	9.0b-g	9.5b-h	9.5b-h
	15	17.3j	11.8f-i	11.5c-i	11.8f-i
	20	X[a]	X	11.3d-i	12.5hi
14	10	8.0b-d	8.0b-d	8.0b-d	9.3b-h
	15	X	X	7.8a-c	6.5ab
	20	X	X	X	4.5a
21	10	X	7.8a-c	7.3a-c	8.8b-g
	15	X	X	X	4.5a
	20	X	X	X	X

Untreated seed--8.8b-g

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A8. Experiment 1: Effect of priming treatment on uniformity of effective germination (days) of seedlot A at 21°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	3.3a-d	3.3a-d	3.0a-d	3.0a-d
	15	3.5b-d	3.3a-d	4.0cd	3.0a-d
	20	4.3d	4.0cd	4.3d	3.5b-d
7	10	3.0a-d	3.3a-d	3.3a-d	2.8a-c
	15	3.0a-d	3.0a-d	3.5b-d	3.8b-d
	20	X[a]	X	3.3a-d	2.5ab
14	10	3.5b-d	3.5b-d	2.8a-c	3.0a-c
	15	X	X	2.8a-c	2.8a-c
	20	X	X	X	2.0a
21	10	X	2.8a-c	2.8a-c	3.3a-d
	15	X	X	X	2.5ab
	20	X	X	X	X

Untreated seed--3.0a

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A9. Experiment 1: Effect of priming treatment on uniformity of effective germination (days) of seedlot A at 32°C germination temperature.

Imbibition time (days)	Imbibition temperature (°C)	Solute concentration (bars)			
		-5.0	-7.5	-10.0	-12.5
3	10	4.3d-g	4.0c-g	4.3d-g	3.5b-f
	15	4.3d-g	4.3d-g	3.8b-f	4.0c-g
	20	5.3gh	4.5e-g	4.5e-g	4.8fg
7	10	4.0c-g	3.5b-f	3.5b-f	4.0c-g
	15	3.5b-f	3.8b-f	3.5b-f	4.0c-g
	20	X[a]	X	3.0a-d	3.5b-f
14	10	3.0a-d	2.8a-c	3.0a-d	3.3a-e
	15	X	X	2.0a	2.8a-c
	20	X	X	X	2.0a
21	10	X	2.5ab	3.0a-d	3.0a-d
	15	X	X	X	2.0a
	20	X	X	X	X

Untreated seed--5.8h

[a] X indicates that at least 10% of the seeds split during priming; consequently, germination tests were not conducted.

There is no significant difference (P = 0.05) between values with the same lower case letter.

Table A10. Experiment 3: Effect of priming treatment on T50 (days) of seedlot A in growth chamber (20°C) and greenhouse environments.

Location	Germination medium	Treatment number			Untreated seed
		3	6	5	
Growth chamber	Peat-vermiculite	6.0a	5.7a	6.0a	9.8b
Growth chamber	Petri dishes	2.8b	2.2a	2.7ab	6.0c
Greenhouse	Peat-vermiculite	5.2a	5.0a	5.0a	8.5b

There is no significant difference at the 5% level between values with the same lower case letter in the same row.

Table A11. Experiment 3: Effect of priming treatment on peak values of seedlot A in growth chamber (20°C) and greenhouse environments.

Location	Germination medium	Treatment number			Untreated seed
		3	6	5	
Growth chamber	Peat-vermiculite	7.2b	7.7c	7.1b	4.5a
Growth chamber	Petri dishes	16.1b	16.9b	16.6b	7.9a
Greenhouse	Peat-vermiculite	7.7b	7.6b	8.0c	5.2a

There is no significant difference at the 5% level between values with the same lower case letter in the same row.